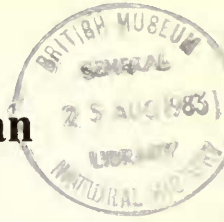


On *Macroleuroodus*, *Chilotilapia* (Teleostei, Cichlidae), and the interrelationships of African cichlid species flocks



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Synopsis

The monotypic cichlid genera *Macroleuroodus bicolor* from Lake Victoria, and *Chilotilapia rhoadesi* from Lake Malawi share an outstandingly derived dentition of a kind not recorded in any other members of the family.

Since both taxa share, uniquely, such a derived character complex, it might be thought that they also share a recent common ancestry not shared with other members of the Lake Malawi and Lake Tanganyika cichlid species flocks. A detailed consideration of other anatomical and morphological features indicates that the dental similarity is a homoplastic feature. However, it seems probable that both taxa are members of a monophyletic lineage within the haplochromine cichlids, and that representatives of this lineage occur in Lakes Malawi, Victoria and Tanganyika.

The features previously used to establish the monophyly of the Lake Malawi haplochromine species are found to be unsuitable for that purpose. Other characters suggest, on the contrary, that the species flocks of Lakes Victoria, Malawi and Tanganyika are each composed of several distinct lineages, and that members of at least some lineages occur in more than one lake.

Introduction

Little attention has been given to the problem of interrelating the endemic cichlid faunas of the major African lakes, Tanganyika, Malawi and Victoria (but see Stiassny, 1981). In part this lack of enquiry can be attributed to the size of the problem, over 500 species are involved, in part to a long established idea that the African cichlids can be separated into haplochromine and tilapiine lineages, hence some similarities were simply ascribed to convergent evolution, and in part to another long standing assumption, that within a lake all the taxa in either lineage are most closely related to one another (hence the greater concern with intra- rather than interlake relationships; Regan, 1920, 1922a & b; Trewavas, 1935 & 1949; Fryer & Iles, 1972; Greenwood, 1974).

Recent investigations have cast considerable doubt on the concept of a simple

haplochromine–tilapiine dichotomy in the phylogeny of African cichlids (see discussions in Fryer & Iles, 1972, and Greenwood, 1978). This changed viewpoint has, in a sense, complicated the issue. Lake Tanganyika species once thought to be tilapiine stock and therefore convergent mimics of haplochromine taxa in Lake Malawi (see Regan, 1922*a*: 675; Fryer & Iles, 1972: 513–8) must now have their phyletic relationships reassessed. Such reassessment also involves species from Lake Victoria because convergence has been invoked to explain similarities between certain species of that lake with others from Malawi and Tanganyika (Regan, 1922*b*: 159). Further complications arise from evidence which suggests that the postulated monophyly of the haplochromine and the tilapiine species in each lake is questionable (Greenwood, 1980), a suggestion which also questions the previously assumed close relationships of the endemic species in a particular lake.

In short, the whole problem of phyletic interrelationships needs critical reexamination in the light of information gathered since Regan's and Trewavas' pioneering researches on these fishes. It also requires, because different levels of relationship are involved, that the search for sister-taxa be extended beyond the confines of a single lake, a possibility that was not critically examined in the past. Then, as more recently (Regan, 1920; 1922*a* & *b*; Trewavas, 1935; 1949; Greenwood, 1974), the tendency has been to identify anatomically generalized 'ancestral' species for each lake fauna, rather than to search for congruent and uniquely shared derived features, synapomorphies, which might indicate common descent irrespective of a taxon's present geographical locality.

On reflection, it would seem that previous surveys have too readily invoked 'convergence' and 'parallelism' to explain similarity between members of different lake faunas, and that the assumptions were made without hard evidence based on critical analysis. Likewise, the mono- or at most, oligophyletic origin of a particular lake's fauna, or elements of its fauna when 'haplochromine' and 'tilapiine' lineages are involved, have also been assumed without sufficient evidence.

Unfortunately, the large number of species involved, coupled with the very disparate levels of information available on the anatomy and ontogeny of those species, requires that a piecemeal approach to the problems be adopted. The limitations and pitfalls of such an approach are serious. But, considering the size of the problem and the need to overhaul the bases for previous and sometimes inhibiting assumptions, even a piecemeal approach can be profitable.

This present paper centres around two monotypic genera, *Chilotilapia rhoadesi* Blgr., 1908, from Lake Malawi, and *Macrolepurodus bicolor* (Blgr) 1906, from Lake Victoria.

Both share a very characteristic dental pattern and tooth form neither of which is found in any other cichlids, either African or American (see Figs 1–10). Ontogenetically, too, they are alike in the way the dental pattern develops, and in having a dental succession involving at least two, and probably three distinct types of teeth. Not surprisingly, larger individuals in both taxa have similar feeding habits. Both crush molluscs between massive jaw teeth before ingesting the soft parts of their prey (Fryer & Iles, 1972; Greenwood, 1956; 1974).

Intergeneric similarities extend beyond these dental and trophic features, although some are certainly correlates. The resemblances include marked similarity in the morphology of the jaws, the syncranial architecture, and in certain myological details.

The two species would almost certainly be placed in single genus if they occurred in the same lake basin. Thus, there would seem to be an *a priori* case for considering the genera to be closely related.

The ranking of *Chilotilapia* and *Macrolepurodus* as distinct and not particularly closely related genera has been influenced by three major considerations. First, the belief that the haplochromine species of any one lake are more closely related to one another than to species from other lakes (Regan, 1922*b*: 165). Second, the idea that, in Lake Malawi, this relationship is manifest in certain marker characters carried by most of its endemic haplochromines including *Chilotilapia* (Regan, 1922*b*: 158; Trewavas, 1949), and thirdly, a misunderstanding by some workers (Trewavas, 1935: 68; see also Fryer & Iles, 1974: 75) about the fundamental nature of the definitive tooth form in *Chilotilapia*.

Regan (1922b: 159) did, however, notice a basic similarity in the dental morphology and pattern of *Macroleurodus* and *Chilotilapia*. But, since he considered the cichlids of Lakes Victoria and Malawi to be but distantly related, and the two taxa to be members of different lineages, it was inevitable that he should attribute their similarities to convergent evolution.

Trewavas (1935: 69–70), on the other hand, recognized that *Chilotilapia* was in fact a member of Regan's haplochromine group, as is *Macroleurodus*, but made no comments on the close similarity of its dentition with that of *Macroleurodus*. Because of its peculiar dentition in relation to that of other endemic Malawi haplochromines, Trewavas maintained the generic status of *Chilotilapia* and suggested on other characters (*op. cit.*: 110), that its nearest living relative was a species in that lake, *Haplochromis euchilus* (see p. 222 *et seq.*).

Before considering these different viewpoints and the whole question of relationships, if any, between the cichlids of Lakes Victoria, Malawi and Tanganyika, detailed comments must be made on the dentition and other anatomical features of both *Chilotilapia* and *Macroleurodus*.

Materials and abbreviations

The entire British Museum (Nat. Hist.) collection of cichlid dry skeletal material and alizarin transparencies used in previous studies on the interrelationships of African haplochromines, was utilized in the preparation of this paper (see Greenwood, 1980; 1983).

Additional dry skeletons were made from:

Macroleurodus bicolor: 1955.2.10:3; 1955.2.10:63–64; 1955.2.10:74–79 two preparations.

Chilotilapia rhoadesi: 1935.6.14: 2121–6; 1935.6.14:2103–2112 three preparations.

Dissections on the jaw and branchial muscles were made on:

Macroleurodus bicolor: 1955.2.10:74–79 three specimens.

Chilotilapia rhoadesi: 1935.6.14:2121–6, and 1935.6.14:2102–2112.

Additional but partial dissections were also made on specimens from this lot.

Dissections of the branchial musculature only were made from:

Astatotilapia burtoni: 1950.4.1:2176–2200

Aulonocranus dewindti: 1960.9.30:4629–4641

Grammatotria lemairei: 1930.4.1:3758–3785

Dissections of the jaw muscles were made on:

Ptyochromis annectens: 1956.10.9:84–87

The use of the letters M, T, or V in parentheses after a generic or specific name indicates the taxon is from, respectively, Lake Malawi, Tanganyika or Victoria. For the purposes of this paper, the haplochromine fauna of Lake Victoria is taken to include that of Lakes Edward and George, Kioga, and Kivu since several of the genera discussed occur in, but only in, all five lakes (see Greenwood, 1980).

All abbreviations used in text figures are amplified in the relevant figure captions.

Dental characters, and their ontogeny, in *Chilotilapia rhoadesi* and *Macroleurodus bicolor*

The definitive, and most characteristic, dentition of *Chilotilapia* (Fig. 3) is apparent only in fishes over 120 mm standard length (SL), but even in smaller fishes the teeth are already distinctive (Fig. 2).

The outer row teeth in both jaws of fishes throughout the size range available, 48–200 mm SL, are mostly stout bicuspid. The minor cusp is small but distinct, the major cusp slightly protracted, the neck nearly cylindrical in cross-section, and the crown somewhat incurved



Fig. 1 *Macrolepurodus bicolor*. Scanning electron micrograph of anterolateral teeth in the outer row of the left premaxilla, seen in labial view ($67.5\times$ N.S.). From a specimen 58 mm standard length.

buccally (Figs 2 & 6). With increasing body size the teeth gradually become stouter, the crown less compressed except at its extreme occlusal edge, and the minor cusp is reduced further, partly it would seem through wear, but also through its absolute reduction in teeth of successive replacement generations.

A second, and essentially tricuspid, tooth type (Fig. 3) first appears in fishes of between 105 and 115 mm SL. Such teeth sometimes predominate in the outer tooth rows of specimens > 140 mm SL; but even when this is so a number of bicuspid teeth persist and may be the predominant form even in fishes as large as 220 mm SL.

In the tricuspid teeth the major cusp is still clearly the largest one, and has virtually the proportions and shape of that cusp in bicuspid teeth but it is slightly more protracted. The two minor cusps are situated at the base of the major one, i.e. are labial in position, are of equal or subequal size, and unless greatly worn, have their rounded tips at the same level as the occlusal surface of the major cusp. A shallow groove, most marked in unerupted and newly erupted teeth, lies between the minor cusps and extends for a short distance onto the occlusal surface of the major cusp.

It is these teeth which Trewavas (1935:67) described as having '... crowns shaped like a grain of wheat. . .' I cannot, however, agree with her statement (*loc. cit*) that in adult fishes all the outer teeth are of this kind. Certainly in some large fishes the majority of teeth is of that kind, but in other and even larger specimens tricuspid teeth are poorly represented. Their number generally increases with the size of the fish; none is present in specimens less than 105 mm SL.

As noted before, the essentially tricuspid nature of 'wheat grain' teeth is most obvious in



Fig. 2 *Chilotilapia rhoadesi*. Scanning electron micrograph of anterior outer row premaxillary teeth situated on either side of the premaxillary symphysis, seen in labial view ($42\times$ N.S.). From a specimen 65 mm standard length.

newly erupted teeth. With wear the distinctiveness of the minor cusps is lost and the groove between them almost obliterated. The tooth then assumed the appearance of a conical unicuspid in which the crown is aligned almost at right angles to the neck. Since, ontogenetically, predecessors of the tricuspid teeth are bicuspid, and since bicuspid occur together with the 'wheat grain' tricuspid, I cannot agree with Fryer & Iles' (1972:75) description of the dentition in *Chilotilapia* as 'basically conical'.

In addition to size-related changes in tooth form, there are similarly correlated changes in tooth alignment (see Fig. 6).

Most specimens less than 95 mm SL have the outer row teeth of the premaxilla arranged so that the occlusal surface of the major cusp is aligned in parallel with the long axis of the bone, the tips of the crowns following one another in a gently curving arc (Fig. 6). Exceptionally, in some fishes from the upper part of this size range, i.e. 80–90 mm SL, the lateral and posterolateral teeth, rarely only the anterior ones, are implanted so that the crown is angled across the long axis of the bone. The tip of the major cusp points medially, that of the minor one labially.

Specimens of standard lengths greater than 95 mm have the crowns of all teeth in the outer premaxillary row directed medially, but with the anterior teeth less angled than the others (Fig. 6).

Changes in the implantation angle of the outer row teeth in the dentary begin at a smaller body size than do those of the premaxilla. At a standard length of *ca* 70 mm the posterior and posterolateral teeth are distinctly angled, although even at a standard length of 110 mm the crowns of the anterior and anterolateral teeth are but slightly displaced towards the mid-



Fig. 3 *Chilotilapia rhoadesi*. Scanning electron micrograph of anterior and anterolateral teeth (outer and some inner rows) of the right premaxilla, seen in oblique and somewhat posterior occlusal view ($11.6 \times$ N.S.). From a specimen 151 mm standard length.

line. In somewhat larger individuals, however, all the outer teeth on the dentary are distinctly angled, the anterior teeth now directed medially at a greater angle than their counterparts on the premaxilla.

It has not been possible to identify the underlying mechanical causes of these shifts in tooth alignment. That is to say, whether succeeding teeth erupt and are then fused to the bone at a different angle from that of their predecessors, or whether teeth already fixed to the jaw undergo a relative change of angle as a result of differential growth changes in the underlying bone. Certain features suggest, however, that differential bone growth may be responsible. For example, changes in the orientation of individual teeth are coordinate over whole sections of the jaw, yet tooth replacement is irregular and should thus lead to individual teeth



Fig. 4 *Macropleurodus bicolor*. Occlusal surface of anterior and anterolateral outer and inner row teeth from the right premaxilla, seen in oblique and somewhat lateral view ($17.0\times$ N.S.). From a specimen 120 mm standard length.

in any one section being at different angles depending on their time of eruption. Also, those areas of the jaw in which the most marked angling occurs are coincident with regions of the bone which undergo the most marked differential growth, that is, expansion and curvature. These regions are the lateral and posterolateral sections of the premaxilla, and the anterior and anterolateral regions of the dentary's alveolar surface.

Teeth forming the inner tooth rows in both jaws also show marked ontogenetic changes in shape and size. The smallest individuals examined, 48–57 mm SL, have mostly small tricuspid teeth in these series, although there are usually a few and slightly larger teeth situated posterolaterally in the premaxilla, where there is but a single inner tooth row. All the inner teeth in fishes of this size group are of the common tricuspid type. That is, with two small lateral cusps flanking a larger central cusp, and the whole crown gently recurved.

Fishes between 60 and 105 mm SL show a gradual replacement of preexisting premaxillary teeth by stouter and coarser ones. Posterolaterally the replacements are bicuspid teeth closely resembling, but smaller than, the teeth of the outer row (see p. 211 above). Elsewhere in the upper jaw the replacements are either stouter versions of the earlier tricuspid teeth, or, more commonly, stout and weakly tricuspid teeth in which the median cusp is so dominant that the tooth is all but unicuspid.

The inner rows of dentary teeth, which are virtually confined to the anterior and anterolateral parts of the bone, undergo similar changes in specimens of the same size ranges. Some 'wheat grain' teeth, smaller versions of those in the outer row, may be present in the outermost series of the inner dentary rows; one exceptional fish has almost the entire outermost row composed of such teeth.

As body growth proceeds beyond about the 100 mm SL mark, so are increasing numbers of inner row premaxillary teeth replaced by bicuspid teeth which, although smaller than those



Fig. 5 *Chilotilapia rhoadesi*. Occlusal surface of anterior and anterolateral outer and inner row teeth on the left premaxilla, seen in oblique and somewhat lateral view ($12.8\times$ N.S.). From a specimen 190 mm standard length.

of the outer row, closely resemble them in gross morphology. Laterally and posterolaterally a few 'wheat grain' teeth make their first appearance in the inner tooth rows of the premaxilla. Only the innermost one or two rows retain small and weakly tricuspid teeth, or an admixture of these with small unicuspid.

In the largest fishes examined, i.e. 160–220 mm SL, the lateral and posterolateral regions of the premaxilla have at least 2 or 3 rows of noticeably enlarged teeth. These may be of the 'wheat grain' type, bicuspid or an admixture of both types.

Noticeably enlarged inner teeth on the dentary of large fishes are confined to the anterior and anterolateral part of the outermost series. However, all teeth in the succeeding rows, except the innermost one and those in the lateral part of the outermost row, are relatively enlarged. Like all inner teeth on this bone, they are slightly smaller than their counterparts on the premaxilla.

The number of tooth rows in both jaws increases, somewhat irregularly, with increasing body length. The smallest specimen examined, 48 mm SL, has 2, in places 3, rows in both jaws, the largest specimen, 220 mm SL, has 5 rows. Specimens in the middle size range may have 3 or 4 rows in each jaw, that number not always correlated with the fish's length.

At first glance, larger fishes seem to have more teeth laterally and posterolaterally in the premaxilla. This, however, is illusory, a result of the teeth in that region of the bone being slightly larger and less closely arranged than elsewhere. In this region too, there is less space between the tips of the teeth, the interspaces between them being taken up by the enlarged crowns. Thus, this area of the premaxillary occlusal surface is, effectively, more compact than it is elsewhere on the bone.

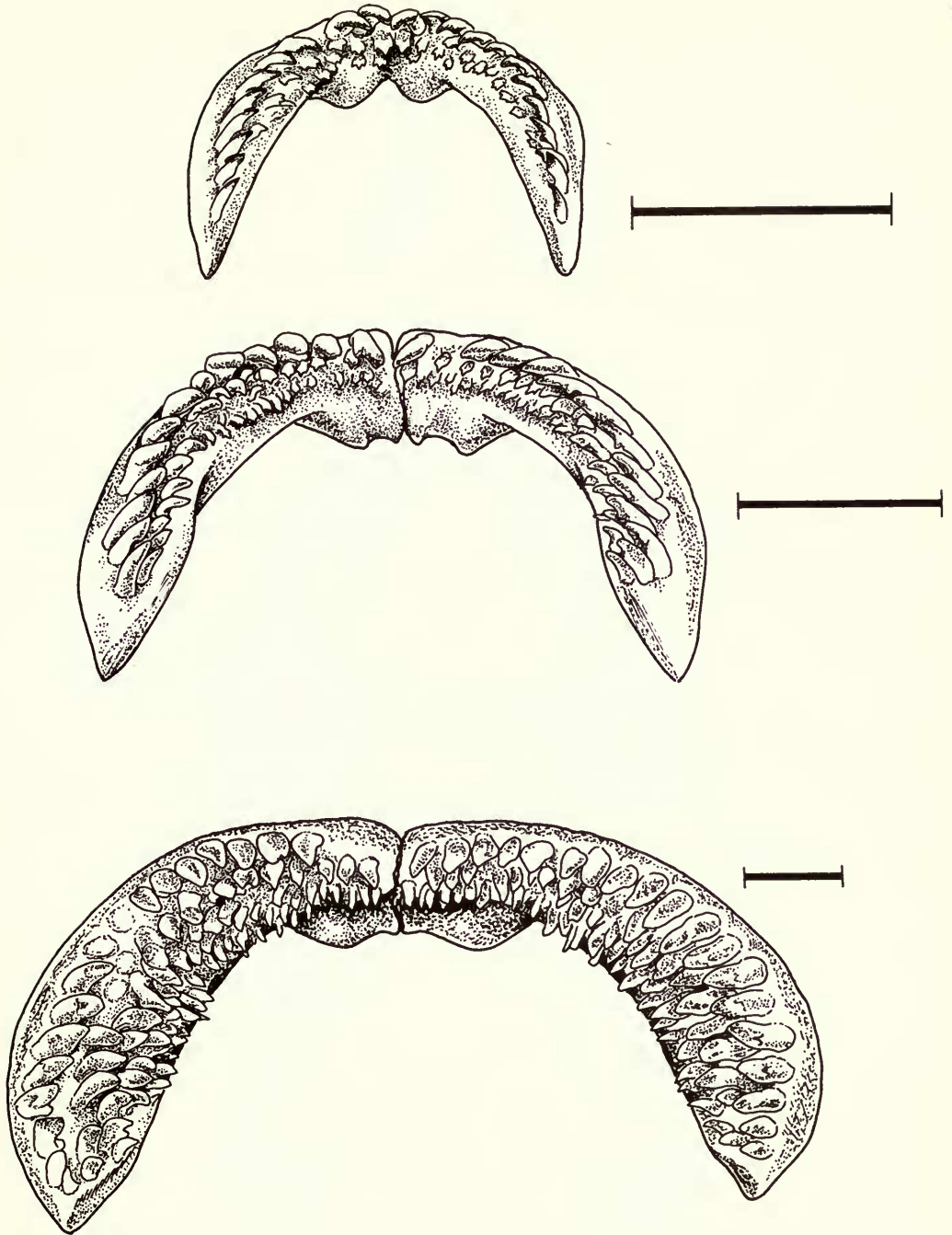


Fig. 6 *Chilotilapia rhoadesi*. Premaxilla showing dentigerous surface in occlusal view; from specimens 65.0 (top) 98.0 and 190.0 mm standard length respectively. Scale = 3 mm.

Tooth number in the outer row of the premaxilla ranges from 20–30 in fishes < 100 mm SL, with fishes in the 48–70 mm range having, in general, 20–24 teeth, and from 24–40 in fishes 105–220 mm SL.

Ontogenetic changes in jaw shape were mentioned earlier (p. 215). These involve, principally, the premaxilla. In the smallest skeleton examined, from a fish 65 mm SL, there is, relative to the generalized condition, an obvious broadening of the premaxilla and its alveolar surface over the lateral and posterolateral extent of the horizontal arms (Fig. 6). This broadening becomes more pronounced with growth, and the widened area extends from its former anterior position to encompass the posterior parts of the arm as well (Fig. 6). Correlated with these changes there is an overall thickening and inflation of the horizontal arms and a change in the outline shape of the entire premaxillary occlusal surface. The latter changes from one which is broadly U-shaped, to one in which the base of the U is flattened and extended laterally (see Fig. 6).

Alterations in the shape and proportions of the dentary are somewhat less pronounced, and involve, mainly, a thickening and outward bulging of the anterior and anterolateral alveolar surfaces and the bone immediately underlying them. There is also a change in occlusal outline correlated with the changing outline of the premaxilla (Fig. 7).

The distinctive dentition, dental pattern and jaw bone morphology characterizing *Chilotilapia* are repeated, with only minor differences, in *Macroleuroodus bicolor*, as are their ontogenies (cf. Figs 1, 4, 8 & 9, with 2, 3, 5, 6 & 7).

Departures from the *Chilotilapia* condition occurring in *Macroleuroodus* are:

1. The major cusp in all bicuspid outer row teeth, and in the definitive tricuspid 'wheat-grain' teeth, is more protracted than in *Chilotilapia* (cf. Figs 3 & 5 with 4). As in that genus, however, the major cusp becomes relatively stouter and almost cylindrical in the largest teeth.
2. The two minor cusps in a 'wheat-grain' tricuspid are lower than in *Chilotilapia*, and the groove between them is shallower. The minor cusps are often worn away in larger fishes.
3. The widened posterior and posterolateral region of the premaxillary alveolar surface in larger fishes is, relatively speaking, slightly narrower in *Macroleuroodus* (cf. Figs 6 & 8).
4. There are fewer inner tooth rows laterally and posterolaterally in the premaxilla of *Macroleuroodus*, usually 1 or 2, compared with 2–5 in *Chilotilapia*; the number in that taxon, but not *Macroleuroodus*, being partially correlated with the fish's size.
5. One or occasionally both arms of the premaxilla are bowed in the vertical plane (see Greenwood, 1956:306–7; 1980:80–81).
6. The different tooth forms, especially the 'wheat-grain' type, first appear in individuals of a smaller size. However, it should be recalled that individuals of *Chilotilapia* reach a larger maximum adult size, at least 220 mm SL, than do those of *Macroleuroodus*, 150 mm SL, modal range 110–130 mm. That *Chilotilapia* has more rows of premaxillary inner teeth (see p. 216) may also be related to the larger adult sizes attained in that genus.

The buccal larvae of *Macroleuroodus bicolor*, at a total length of about 9.0 mm, have slender and conical outer teeth in both jaws (Greenwood, 1956: 308). Similar teeth occur in the buccal larvae of *Astatotilapia macrops* at a comparable developmental stage; adults of that species have the generalized bicuspid tooth type found in many haplochromine cichlids (see Greenwood, 1979 & 1980). Unfortunately no larval *Chilotilapia* are available for examination.

Compared with intergeneric dental differences in other cichlids, those distinguishing *Chilotilapia* and *Macroleuroodus* are very slight. Indeed, they are of a kind which, on current taxonomic practice, would not be rated at more than 'specific-differences' if the two taxa were sympatric.

From a phylogenetic viewpoint these uniquely shared and derived dental features of *Chilotilapia* and *Macroleuroodus* would seem to indicate a recent common ancestry for the two taxa. To test that hypothesis, which contradicts current views on the relationships of the two genera, see p. 211 above, a search was made for characters that might refute it.

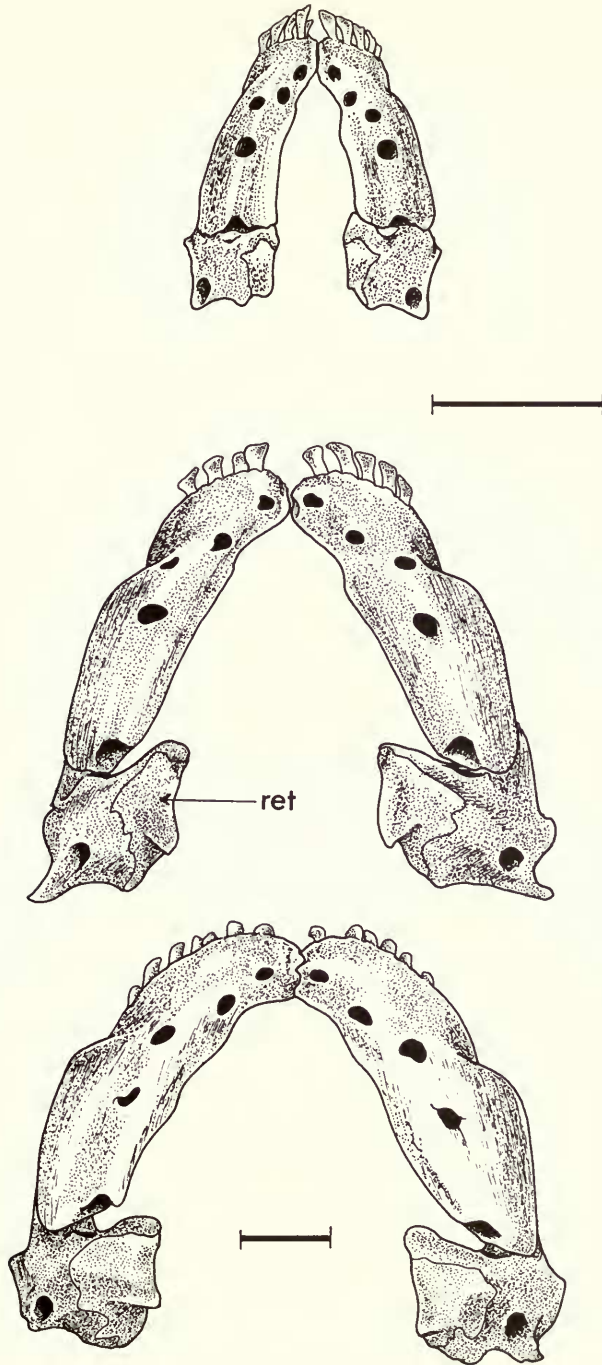


Fig. 7 *Chilotilapia rhoadesi*. Lower jaw in ventral view; from specimens 65.0 (top) 98.0 and 190.0 mm standard length respectively. ret = retroarticular. Scale = 3 mm.

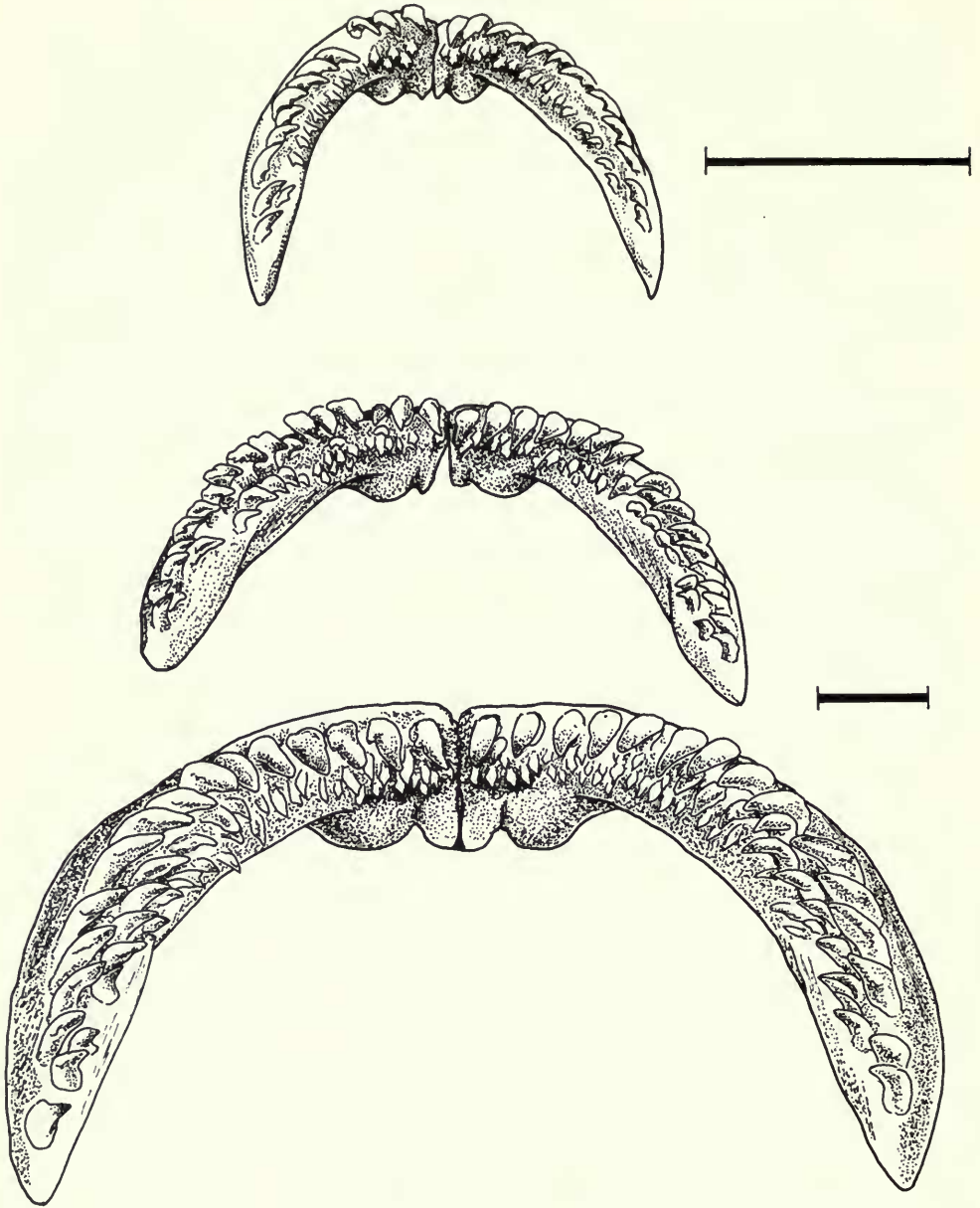


Fig. 8 *Macrolepurodus bicolor*. Premaxilla, showing dentigerous surface in occlusal view; from specimens 58.0 (top), 115.0 and 144.0 mm standard length respectively. Scale = 3 mm.

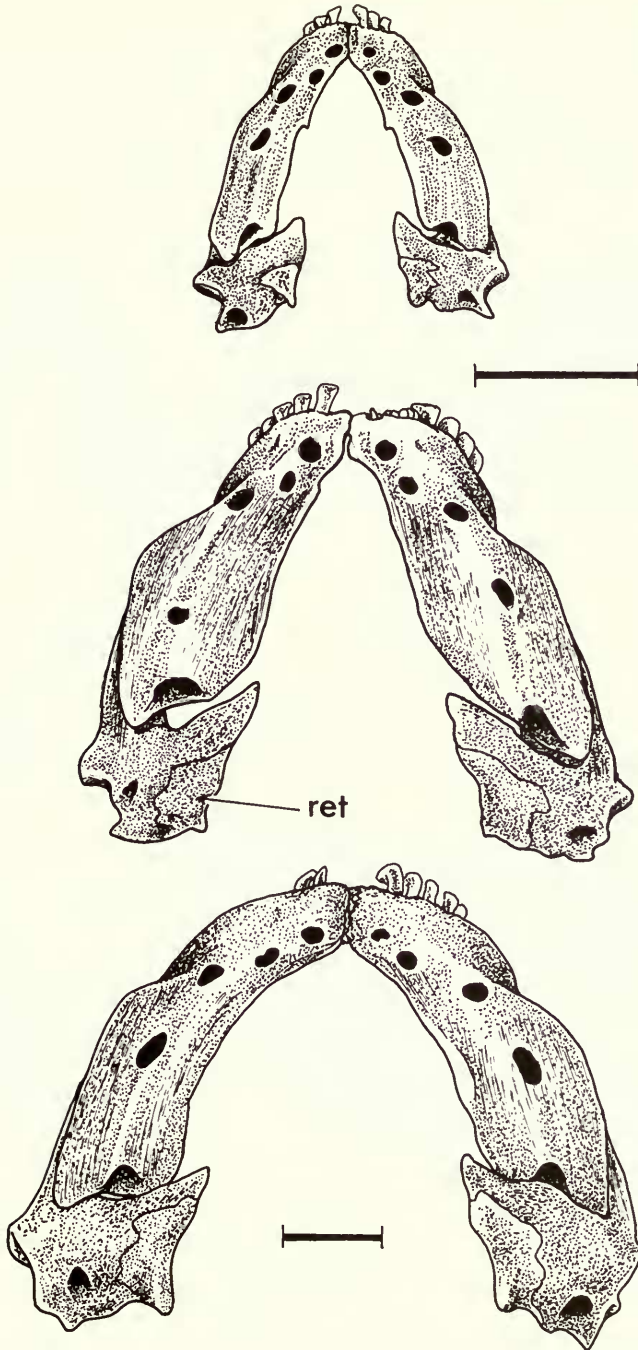


Fig. 9 *Macropleurodus bicolor*. Lower jaw, in ventral view; from specimens 58.0 (top), 115.0 and 144.0 mm standard length respectively. ret = retroarticular. Scale = 3 mm.

**A comparison and assessment of other anatomical features in
Macroleuroodus bicolor and *Chilotilapia rhoadesi***

The superficial characters, body form and meristic characters of the two taxa (see Boulenger, 1915; Regan, 1922a), apart from the densely and almost completely scaled caudal fin in *C. rhoadesi*, and differences in coloration, do not provide any features of value for testing a hypothesis of close relationship.

The caudal fin character, which Regan (1922a & b) and Trewavas (1949) used as evidence for close interrelationship of the Malawi haplochromines and their distinctness from those of Lake Victoria, will be discussed later (p. 228).

In their live coloration (see Greenwood, 1956:308–310 for *M. bicolor*; Axelrod & Burgess, 1977:176–177 for *C. rhoadesi*), and in the colour-patterns of preserved specimens (Greenwood, 1956:308–310; Trewavas, 1935:110) the taxa are quite distinct. Trewavas (1935:110) suggested that the colour pattern of *C. rhoadesi* might indicate its relationship with another Malawian endemic, *Haplochromis euchilus* Trewavas. This feature will be discussed later, together with Regan's ideas on colour-patterns as indicators of a monophyletic origin for the Malawi haplochromines (Regan, 1922a:686).

Macroleuroodus bicolor exhibits a form of sex-limited polychromatism in which about 30 per cent of females have a piebald coloration (Greenwood, 1956:309). Similar polychromatism occurs in several endemic species of Lake Victoria haplochromines, not all of which appear to be closely related to one another or to *Macroleuroodus* (Greenwood, 1974:53–54;

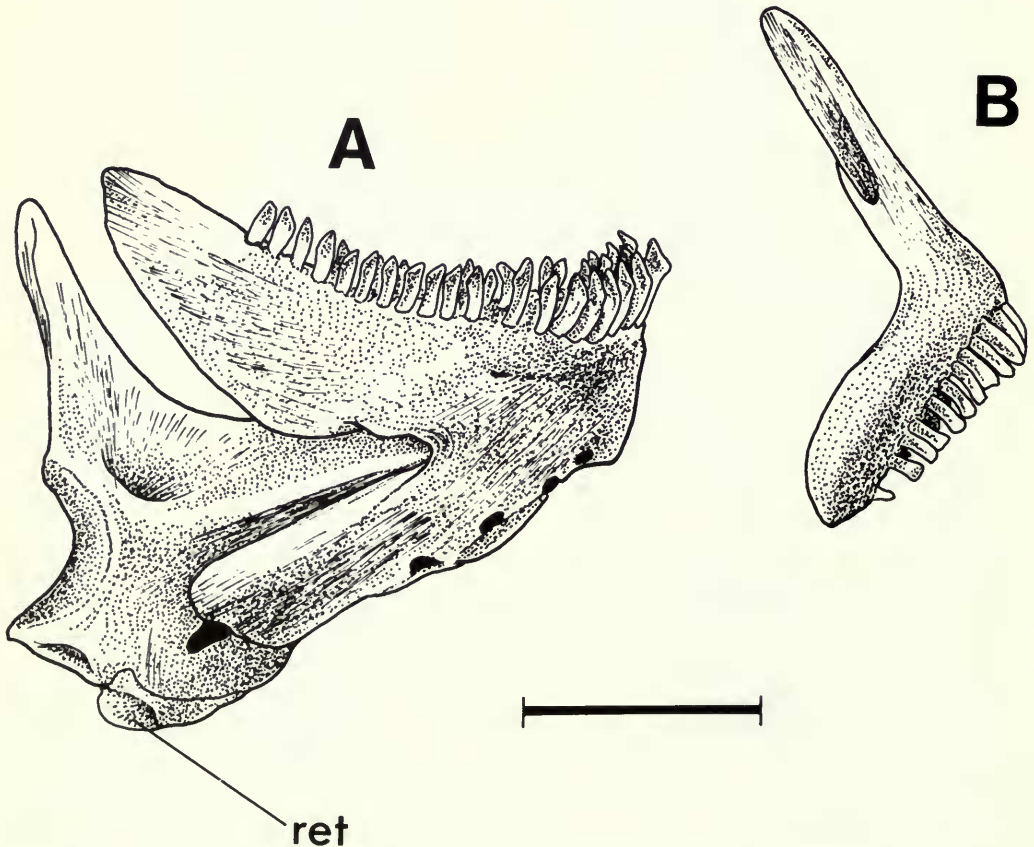


Fig. 10 *Chilotilapia rhoadesi*. A. Dentary and B. Premaxilla; both in right lateral view. ret = retroarticular. Scale = 3 mm.

also 1980, for revised views on the relationships of the various species). Sex-limited polychromatism, involving both similar and different colour patterns, has also been recorded in several Malawi endemics (Fryer & Iles, 1972) but not in *Chilotilapia*.

Adult male *Macrolepurodus* have, on the anal fin, a number of scarlet 'egg-dummies' of the true ocellar type (see Greenwood, 1979:274–5). As far as I can tell from colour photographs and from written descriptions, true ocellar markings are lacking in male *Chilotilapia*. Instead, the anal fin carries a few yellowish spots resembling those on the dorsal and caudal fins, a not uncommon condition amongst Malawi haplochromines, but one not recorded in Lake Victoria.

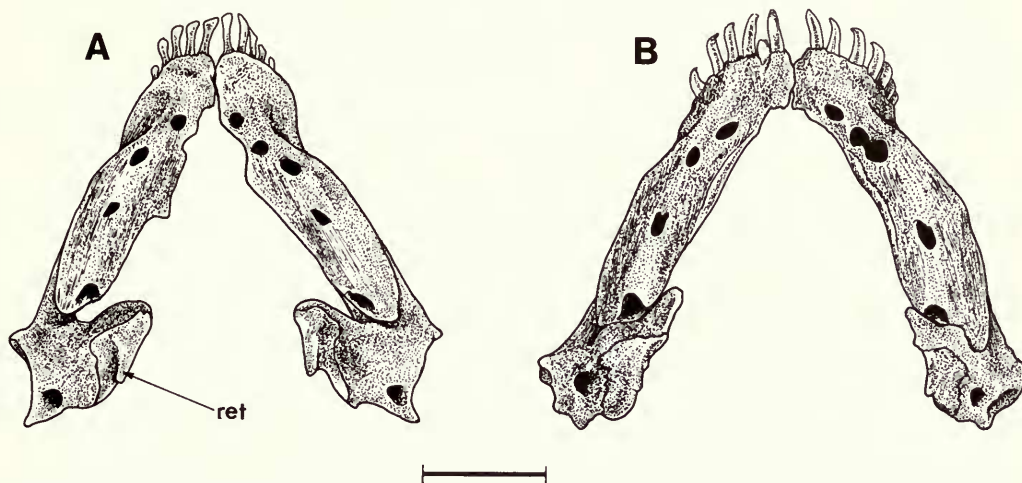


Fig. 11 Lower jaw, in ventral view, of: left, *Paralabidochromis crassilabris* (105 mm standard length); right, '*Haplochromis*' *euchilus* (91 mm standard length). ret = retroarticular. Scale = 3 mm.

At a deeper anatomical level, intergeneric comparisons were made of the jaw and branchial musculature, and of the cranial and axial skeletons. The latter will be considered first.

There is a close similarity in the morphology of the dentary and premaxilla in *Chilotilapia* and *Macrolepurodus*, as there is in the form of the maxilla, a stout and somewhat foreshortened bone in both genera.

The dentary (Fig. 10) too is short, deep and stout, with a noticeably inflated region surrounding its division into ascending, coronoid, and horizontal arms. The principal intergeneric difference lies in the greater posterior extension of the outer tooth row in *Chilotilapia*, the row continuing backwards to a point almost two-thirds of the way up the coronoid process. In *Macrolepurodus* the teeth do not extend, or extend for only a short distance, onto the process.

The premaxilla (Fig. 10) is basically similar in both genera, although in *Macrolepurodus* the dentigerous arm is somewhat less inflated. Also, in that genus one or both dentigerous arms are distinctly arched in the vertical plane (see Greenwood, 1956:306–7; 1980:83); this apparently is an autapomorphy peculiar to *Macrolepurodus*.

Certain derived features in the dentary of *Chilotilapia* and that of *Macrolepurodus* are shared with some Malawi taxa, ('*Haplochromis*' *euchilus* Trewavas [see first para. p. 228] and various *Labidochromis* species), with members of the *Paralabidochromis*–*Ptyochromis* lineage in Lake Victoria (see below), and with at least one species, *Lobochilotes labiatus* Blgr, from Lake Tanganyika.

These derived features, discussed by Greenwood (1980:93–94), are concerned chiefly with the foreshortened lower jaw, the marked bullation of the dentary in the area surrounding

its bifurcation (see above), the pronounced medial curvature of its lateral walls, and the way in which the anterior part of the outer tooth row has a strong ventral dip in its line of insertion on the bone.

In Lake Victoria, these characters are shared by members of a lineage which includes *Macroleuroodus* and the genera *Paralabidochromis* and *Ptyochromis*. These taxa, in turn, are part of a larger group, the so-called *Psammochromis-Macroleuroodus* superlineage (Greenwood, 1980:93–94).

Resemblances in lower jaw form between *Chilotilapia* and *Macroleuroodus* on the one hand, and the various Malawi, Victoria and Tanganyika taxa on the other, are most apparent when specimens of *Chilotilapia* and *Macroleuroodus* less than 70 mm SL are used as a basis for comparison, irrespective of specimen size in the other species involved. Within the Lake Victoria lineage, overall resemblance with *Chilotilapia* and *Macroleuroodus* is closest when comparisons are made with members of the genus *Paralabidochromis* (Fig. 11), less so when the species of *Ptyochromis* are used (see Greenwood, 1980:60–72; 92–94). A level of similarity equal to that existing with *Paralabidochromis* is found when small *Chilotilapia* and *Macroleuroodus* are compared with specimens of various *Labidochromis* species, '*Haplochromis*' *euchilus* and *Lobochilotes* (Fig. 11).

With growth, the dentary in both *Chilotilapia* and *Macroleuroodus* changes its outline shape (see above, p. 218), and thus, superficially, comes to resemble less closely the dentary in these other species. The other derived features remain unaltered, however.

In the ontogeny of their jaws, at least over the size range of available specimens, *Chilotilapia* and *Macroleuroodus* could be described as passing first through a *Paralabidochromis-Labidochromis* stage and then an '*H. euchilus-Lobochilotes*' stage. From that point onwards the jaws in *Chilotilapia* and *Macroleuroodus* begin to broaden anteriorly, taking on the wide-based U shape characteristic of the adults in both taxa. Simultaneously the autapomorphic features of each genus begin to be manifest (see above p. 223).

Neurocranial shape and architecture is similar in *Chilotilapia* and *Macroleuroodus*, but with the former having a taller and more expansive supraoccipital crest. The crest also con-

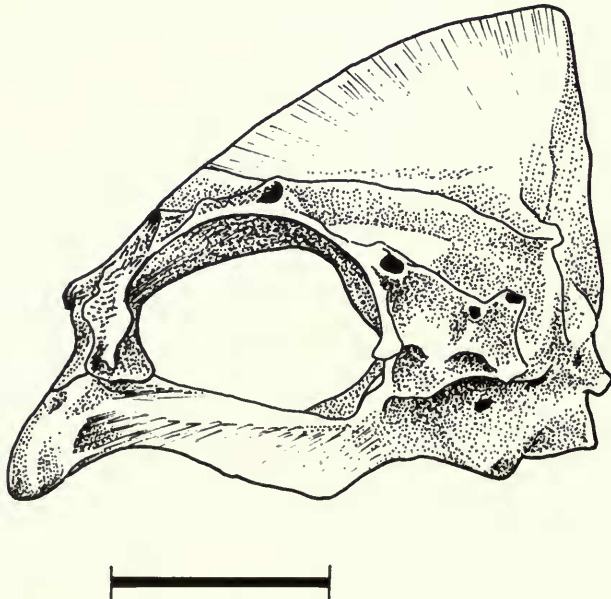


Fig. 12 *Chilotilapia rhoadesi* Neurocranium in left lateral view. Scales = 10 mm.

tinues further forward than it does in *Macropleurodus*, with the result that the slope of its anterior margin is continuous with the slope of the ethmovomerine skull region (Fig. 12); in *Macropleurodus* this line is interrupted (cf. Fig. 12 with fig. 54 in Greenwood, 1980).

The *Macropleurodus*-*Chilotilapia* skull can be considered derived relative to that in *Astatotilapia* species and in several cranially generalized haplochromine lineages (see Greenwood, 1979; 1980). It approximates closely to the skull form in some *Ptyochromis* species of Lake Victoria, e.g. *P. annectens* (Regan), *P. sauvagei* (Pfeffer), and *P. granti* (Blgr). *Ptyochromis*, it will be recalled, is a member of the *Psammochromis*-*Macropleurodus* superlineage to which the genus *Paralabidochromis*, mentioned above in connection with lower jaw morphology, also belongs. Like *Ptyochromis*, both *Chilotilapia* and *Macropleurodus* are mollusc-eaters which 'shell' their prey orally (see Fryer & Iles, 1972:75; Greenwood, 1956; 1974:69-72; 1980:60-67). Thus, jaw form and skull shape in all these species could well be correlated characters forming part of a functional unit. The similarities in jaw morphology existing between non-mollusc eating members of the *Psammochromis*-*Macropleurodus* superlineage (i.e., in this context, the *Paralabidochromis* species), '*Haplochromis*' *euchilus*, the *Labidochromis* species and *Lobochilotes labiatus* on the one hand, and *Macropleurodus* and *Chilotilapia* on the other, are not susceptible to this explanation.

There has, in the past, been some confusion about the nature of the pharyngeal apophysis in *Chilotilapia* (see Regan, 1922a:676; Trewavas, 1935:69-70; Greenwood, 1978:316). The growth series of *Chilotilapia* neurocrania now available help both to clarify that situation and to weaken further the idea of a rigid division between the '*Haplochromis*' and '*Tilapia*' apophyseal types (see discussion in Greenwood, 1978:321).

In a *Chilotilapia* skull of 16 mm neurocranial length, i.e. skull length measured from the anterior tip of the vomer to the posterior face of the basioccipital condylar surface, the apophysis is structurally intermediate between the '*Tilapia*' and the '*Tropheus*' types defined by Greenwood (1978:299-305). Its articulatory facet is formed from the parasphenoid with a small contribution from the basioccipital. The latter, however, has a rounded surface and thus does not seem to form part of the functional articulatory surface. The basal part of the apophysis, i.e. the prootic and basioccipital, is rather inflated; when viewed from behind the entire structure is low and broad.

At a neurocranial length of 23 mm, the apophysis is intermediate between the '*Tropheus*' and '*Haplochromis*' types. The basioccipital makes a small but definite contribution to the articulatory surface (about a third of its area), and the apophyseal base is narrow and less inflated than in the 16 mm skull.

In the largest skull examined, 39 mm neurocranial length, the basioccipital contribution to the articular surface has increased somewhat so that the surface is clearly of the '*Haplochromis*' type (see also Greenwood, 1978:316), as is the narrow, near-vertically walled apophyseal base formed from the prootic and basioccipital.

The apophysis in the smallest available skull of *Macropleurodus*, 20 mm neurocranial length, has an articulatory surface of the '*Haplochromis*' type, although the base of the apophysis is somewhat inflated. In larger skulls, to 25 mm neurocranial length, the base narrows, its walls become more nearly vertical, and there is an increase in the extent to which the basioccipital contributes to the articulatory surface.

The palatopterygoid arch and the suspensorium are similar in *Chilotilapia* and *Macropleurodus*, although both are relatively deeper in *Macropleurodus*. The palatopterygoid arch, when compared with that in *Astatotilapia* and in many other haplochromines, is derived. It is foreshortened, with the lateral face of the metapterygoid deeply concave over most of its area. Like other derived features of the syncranial architecture, this form of palatopterygoid arch occurs in several Lake Victoria species belonging to the *Ptyochromis*-*Paralabidochromis* assemblage, as well as in *Hoplotilapia retrodens*, another member of the *Psammochromis*-*Macropleurodus* superlineage; Greenwood, 1980:82. It is also found in certain Lake Malawi taxa, e.g. *Labidochromis* and *Cyathochromis*, and in some species from Lake Tanganyika as well.

Judging from that pattern of distribution, it seems that this type of palatopterygoid arch is one correlated with a foreshortened skull and the development of a powerful *adductor mandibulae* muscle complex.

The total number of vertebrae, excluding the fused $PU_1 + U_1$ elements, has the same range, 29 or 30, mode 30, in both genera. However, in the samples examined, *Chilotilapia* has modal counts of 14 abdominal and 16 caudal centra, compared with 13 and 17 centra respectively in *Macrolepurodus*.

Myologically, the jaw and branchial musculature, and the associated ligaments in both *Chilotilapia* and *Macrolepurodus* are similar, and are close to the presumed generalized condition found in *Astatotilapia elegans* (see Anker, 1978; Stiassny, 1981; Greenwood, 1983).

The A_1 and A_2 divisions of the *adductor mandibulae* muscle complex in *Chilotilapia* and *Macrolepurodus* are relatively stouter than those in *A. elegans*, but are comparable with the condition found in *Ptyochromis* species, which taxa are also oral-shelling mollusc eaters (Greenwood, 1974; 1980).

The A_3 division of the *adductor mandibulae* in *Chilotilapia* is more slender than in *Macrolepurodus*, and its outline is bobbin-shaped rather than triangular.

Chilotilapia differs from *Macrolepurodus* in having three rather than two divisions to the ethmo-palatine ligament. *Macrolepurodus*, like the majority of Lake Victoria haplochromines, has the long posterior division of the ligament running from the palatine bone to the posterior, i.e. orbital, face of the lateral ethmoid, and the shorter division running to the anterior face of that bone. In *Chilotilapia*, a third division lies between the other two, whose attachments are as in *Macrolepurodus*, and attaches to the ventral face of the lateral ethmoid.

There is little comparative information on these ligaments in cichlid fishes, and thus the significance of their intergeneric differences cannot be assessed. A tripartite ethmo-palatine ligament does occur in several Malawi taxa I examined, and in some Tanganyika species as well. The condition is rarely encountered in Lake Victoria haplochromines although, and perhaps significantly, it is present in one oral-sheller, *Ptyochromis annectens* (Regan).

Gill-arch musculature in *Chilotilapia* and *Macrolepurodus* is of the generalized type (see Liem, 1981; Greenwood, 1983). There are slight differences in the degree to which certain muscles are developed in the two genera. The *levator externi*, especially the fourth pair, are larger in *Chilotilapia*, and the *transversus dorsalis epibranchialis 2* is more tendinous in *Macrolepurodus*. Both genera have the first *levator externi* muscles well-developed, with musculose rather than tendinous insertions.

Because relatively little information is available on the comparative myology of the Cichlidae, the information derived from *Chilotilapia* and *Macrolepurodus* provides no data of positive value in a phylogenetic context. Negatively, however, since their myology compares closely with the generalized condition, it is possible to say that no uniquely apomorphic features are shared by the two genera.

Indeed, the same can also be said for the apomorphic osteological features discussed earlier; all are found in other taxa from Lakes Malawi, Tanganyika and, especially, in species from Lake Victoria. This rather skewed geographical pattern of apomorphy distribution could, however, be artefactual since more is known about the osteology in species from Lake Victoria than in those from the other lakes.

Be that as it may, the only derived features uniquely shared by *Chilotilapia* and *Macrolepurodus* are those relating to tooth morphology and dental patterns in adult and near-adult fishes (see pp. 211–218).

Since these dental apomorphies apparently are not congruent with any other derived characters uniquely shared by the two taxa, they cannot be considered homologous, i.e., true synapomorphies, and must therefore be treated as homoplasies (see discussion in Patterson, 1982).

It remains to be determined whether these homoplasies resulted from parallel or from convergent evolution, and also to assess what phylogenetic significance can be given to those

apomorphic features shared by *Chilotilapia*, *Macropleurodus* and the other taxa mentioned above.

Discussion and conclusions

Before considering these various issues, it is necessary to review current ideas on the origin and relationships of cichlids from Lakes Malawi, Victoria and Tanganyika.

Prior to Regan's (1920; 1922*a* & *b*) revisionary studies on these fishes, and his fundamental reorganization of their generic classification (Regan, 1920), no meaningful speculations or hypotheses could be generated about the origin and relationships of the lake flocks.

Regan based his supraspecific grouping of African cichlids on the nature of the neurocranial apophysis on which the upper pharyngeal bones articulate, a scheme he first worked out on the taxa from Lake Tanganyika (Regan, 1920). On the basis of this character, the majority of Malawian and Victorian species were placed in Regan's '*Haplochromis*' division. The Lake Tanganyika species, on the other hand, were more equally shared between this division and the so-called '*Tilapia*' one. Since Regan considered these two divisions represented a fundamental dichotomy in the phylogeny of the Cichlidae, his views on the relationship of taxa, endemic and otherwise, from the three lakes were influenced accordingly. In particular this meant that resemblances between any member of the '*Tilapia*' group and another of the '*Haplochromis*' group could only be interpreted as the result of convergent evolution.

Trewavas (1935) followed Regan's scheme of supraspecific grouping when she revised the Malawi cichlids, although she transferred four taxa, one of which was *Chilotilapia*, from the '*Tilapia*' to the '*Haplochromis*' division.

Recent research (Wickler, 1963; Fryer & Iles, 1972; Liem & Stewart, 1976; Greenwood, 1978, 1983) strongly indicates that a basic phylogenetic division of African cichlids on apophyseal structure cannot be substantiated (see also observations on the apophysis in *Chilotilapia*, p. 225 above).

Abandoning the pharyngeal apophysis as a critical character for determining major cichlid groupings has, in fact, little effect on the problem of *Chilotilapia*-*Macropleurodus* interrelationships since definitive apophyseal structure in both genera is of the '*Haplochromis*' type. It does, however, affect problems concerned with the relationship of other closely similar taxon pairs, or trios, shared between Lakes Malawi, Victoria and Tanganyika. As examples of taxa whose phyletic status requires reexamination on the basis of other features, one can cite the supposedly convergent *Petrotilapia* (M) and *Petrochromis* (T), *Tropheus* (T) and *Labeotropheus* (M), and *Lobochilotes* (T), '*Haplochromis*' *euchilus* (M) and *Paralabidochromis chilotes* (V).

Regan (1922*b*:158), working within the framework of his strictly dichotomous divisions of the cichlids, believed . . . 'The indications are that the endemic Nyassa (= Malawi) cichlids have originated in the lake from about half-a-dozen ancestral forms'.

Later, Trewavas (1949) supported Regan's concept of an oligophyletic origin for these fishes. After quoting Regan's statement reproduced above, she carried the argument further by concluding, with regard to the endemic Malawian genera, that the ' . . . balance of evidence (is) in favour of Nyassa relationship for all of them'. Indeed, Trewavas (*op. cit.*) specifically rejects Myer's (1936) suggested relationship of the Malawian genus *Pseudotropheus* with the Tanganyika *Simotes*, because the two taxa have different types of pharyngeal apophyses.

Regan (1922*a* & *b*) did not discuss the possible interrelationships of his suggested 'half-a-dozen' ancestral species. He did, however, consider that the numerous endemic '*Haplochromis*' species of Lake Malawi ' . . . appear to form a natural group and have evidently evolved in the lake from one or a few ancestral forms' (Regan, 1922*b*:158). This idea was based largely on one feature which, as far as Regan could ascertain, was shared by most Malawi '*Haplochromis*' species, namely a caudal fin densely covered in small scales. Regan contrasts this condition with that in the '*Haplochromis*' species of Lake Victoria where the ' . . . caudal fin is scaly only on its basal half'.

The genus *Haplochromis* has now been restricted to five species, none of which occurs in Lake Malawi (Greenwood, 1980). No attempt has yet been made to subdivide the Malawian species formerly classified in *Haplochromis*; these are referred to here under the epithet '*Haplochromis*'.

In support of his ideas about the Malawi '*Haplochromis*' species being a natural group, Regan (*op. cit.*) drew attention to the fact that the caudal fin in these species is more or less distinctly emarginate (rounded or truncate in Victoria species) and that a few distinctive types of coloration, none of which occurs in Lake Victoria, are prevalent amongst the Malawi fishes. Here again, Trewavas (1935; 1949) accepted Regan's arguments, and expanded the scope of the supposed natural group defined by these characters to include the endemic haplochromine genera of Lake Malawi. Thus, at least by implication, all the haplochromine taxa of Malawi were assumed to be members of a natural group. From this it would follow, again by implication, that the ancestral forms were more closely related to one another than to any other taxa. Also, but neither Regan nor Trewavas is explicit on this point, the argument would assume the caudal fin characters to have evolved within the Lake because no extant fluviatile species show these features. Trewavas (1949) does, however, note, but makes no further comment on, the absence of a fully scaled caudal fin in '*Haplochromis callipterus* (Günther), a species which she thought to be a likely representative of the '... ancestor of many (*Haplochromis*)' species of Nyasa'.

The validity of the caudal fin characters as evidence for a natural group in Lake Malawi is weakened by a fact which neither author mentions, that is, the occurrence of a densely and completely, or almost completely, scaled caudal fin in several endemic Tanganyika genera, some of which also have the fin forked or emarginate, e.g. *Petrochromis*, *Simochromis*, *Tropheus*, *Lobochilotes*, *Eretmodus*, *Lamprologus*, and *Cyphotilapia*; personal observations based on a by no means comprehensive sample of the Lake Tanganyika species. Interestingly, four of these Tanganyika genera have been associated in a 'convergent' relationship with taxa from Lake Malawi (see above, p. 227).

Finally, and perhaps most significantly, it must be noted that the four endemic species of *Oreochromis* (= *Tilapia* of Trewavas, 1935 & 1949) in Lake Malawi also have densely and completely scaled caudal fins. None of these species is in any way closely related to the Malawi haplochromines.

Such a character distribution pattern, and especially its inclusion of the endemic Malawi *Oreochromis* species, would seem to invalidate the character's use as a means of identifying the Lake Malawi haplochromines as a 'natural group'.

The shape of the caudal fin margin is also of doubtful validity in this context. To start with, it shows a quite considerable range of variation within the Malawi taxa, in some of which the nature of the fin margin scarcely differs from the condition found in certain Lake Victoria species. In that Lake, *pace* Regan, a rounded caudal margin is rare, the modal condition ranging from subtruncate to truncate; a few species even have a slight but distinctly emarginate fin (compare figures in Greenwood, 1982a with those in Regan, 1922a). Truncate and emarginate fins, as well as subtruncate and rounded ones, occur amongst the Lake Tanganyika endemics, sometimes with more than one type present in a single genus.

Again, one is apparently faced with a character of doubtful phylogenetic validity. Not only is this so for the reasons given above but, like the scaly caudal fin, because it is not congruent with other and well-substantiated synapomorphies shared by the various taxa involved.

The absence of a fully scaled caudal fin amongst the Lake Victoria cichlids, contrasted with the near universal occurrence of that trait in Malawi cichlids, and its presence among some but not all Tanganyika taxa, nevertheless requires explanation. The answer, however, like that explaining the occurrence of predominant but different kinds of caudal fin margins in each of the different lakes, is unlikely to be provided by the data currently available.

Regan's (1922a:686) view that the prevalence of a few distinctive types of coloration among the Malawi haplochromines corroborated the other indications of their evolution '... within the lake from a single ancestral form ...', can also be challenged. Granted, there

are distinctive colour patterns, i.e. striping, barring etc., and some distinctive types of overall coloration not found in the fishes of Victoria or Tanganyika. But, since these features are not shared by every member of the Malawi flock, they cannot be taken to indicate monophyly for all the species of the Lake. Their value as indicators of relationship lies at a much lower level of universality.

The absence of true anal ocelli in male *Chilotilapia*, and in most Malawi haplochromines, contrasted with their presence in males of, apparently, all Victoria haplochromines, poses an insoluble question with regard to phylogenetic histories (see Greenwood, 1979:274–276). It is a character that has not yet received sufficient study to permit its evaluation in that context. Whether true ocelli be a derived or a plesiomorphic feature, the fact that both ocellar and non-ocellar anal markings are present in Malawi haplochromines would argue against a monophyletic origin for the flock as a whole.

In short, I would suggest that none of the characters so far proposed in support of a mono- or even oligophyletic origin for the Malawi haplochromines is valid for that purpose. Since, despite an extensive search, I can find no valid characters to replace them, the case for a monophyletic origin of the Malawi haplochromines must, for the moment, remain unsubstantiated.

Research on the haplochromines of Lake Victoria has also failed to reveal a single synapomorphy indicative of a monophyletic origin for those taxa either (Greenwood, 1979; 1980). What is suggested, however, is the presence of several distinct monophyletic lineages whose distributions include not only Lake Victoria but Lakes George, Edward and Kivu as well. Each of these lineages is distinguished by, at best, two or three synapomorphies. In other words, there is a low level of interlineage differentiation, with the residual, i.e. plesiomorphic, characters being common to most haplochromine taxa whatever their geographical distribution may be.

Perhaps significantly, it is with one of the Victoria lineages, the *Paralabidochromis-Ptyochromis-Macropleurodus* complex within the *Psammochromis-Macropleurodus* superlineage, that *Chilotilapia* shares the greatest number of apomorphic characters (see Greenwood, 1980:91–94; & p. 223 above). Furthermore, there are at least two taxa in Lake Malawi, *Labidochromis* and '*Haplochromis*' *euchilus*, and one from Lake Tanganyika, *Lobochilotes labiatus* Blgr, which also share a number of these features. In none of these latter taxa can I identify any synapomorphies shared with Lake Victoria lineages other than the *Paralabidochromis-Macropleurodus* one, nor any which might suggest a relationship, above the sister-species level, with taxa from, respectively, Lake Malawi or Lake Tanganyika.

Parenthetically it should be noted that some of the oral features shared by these taxa also occur in two other Lake Victoria lineages, namely *Neochromis* and *Lipochromis* (see discussion in Greenwood, 1980: 52 & 91–94; also p. 223 above). It has been argued (Greenwood, *op. cit.*) on the basis of derived dental features shared by members of the *Psammochromis-Macropleurodus* superlineage, and others uniquely characterizing *Neochromis* and *Lipochromis*, that the similarities in jaw morphology shared by these two taxa with members of the former group were independently evolved. Since the derived dental features of the *Psammochromis-Macropleurodus* group taxa are manifest in *Labidochromis*, '*H. euchilus*', *Lobochilotes* and *Chilotilapia*, the same argument, that is convergence, can be applied to account for their similarities in jaw morphology with *Neochromis* and *Lipochromis*.

Work in progress supports the suggestion of several derived characters being shared by the supposedly 'convergent' Malawi–Tanganyika taxon pairs mentioned on p. 227, and thus that they too may be more closely related than was previously thought. Here, however, it has so far proved impossible to identify any association with a particular lineage from Lake Victoria.

In view of these character distribution patterns, and because the hypothesized monophyletic origin for each lake flock cannot be substantiated, consideration should be given to an

alternative hypothesis. Namely, that the flocks are of polyphyletic origin and that many of the lineages within a flock occur in more than one lake. The pattern of apomorph character distribution in, for example, *Macropheurodus* (V), *Chilotilapia* (M), '*Haplochromis*' *euchilus* (M) and *Lobochilotes* (T) would be explicable on that basis.

Since Lakes Victoria, Malawi and Tanganyika are of different ages (Greenwood, 1982b) and are geographically distant from one another, it is probable that the progenitors of the lineage representatives in each lake would have been different but closely related species. This evolutionary pattern would mean that, despite the ultimate monophyly of a lineage, at the lowest hierarchical levels sister taxa would occur sympatrically. For example, the Lake Victoria members in the lineage cited above would be more closely related to one another than to species in the other lakes, and similarly for the taxa from Malawi and Tanganyika.

On the basis of that argument, the homoplastic dental resemblances between *Chilotilapia* and *Macropheurodus* (see p. 218) are parallelisms, and the nearest relatives of the two taxa should be found in Lakes Malawi and Victoria respectively.

As has already been suggested, the relationships of *Macropheurodus* are apparently with *Paralabidochromis* and *Ptyochromis*, although, for the moment no finer resolution is possible (see Greenwood, 1980:92).

The closest relatives of *Chilotilapia* would, in my view, seem to be *Labidochromis* and, as Trewavas (1935:110) suggested, '*Haplochromis*' *euchilus*. Again, any finer resolution must await further research, as must the resolution of relationships for *Lobochilotes labiatus*, at present seemingly the sole representative of the lineage in Lake Tanganyika.

If this scheme of relationships is accepted, then the generic status accorded to *Chilotilapia* and *Macropheurodus* by earlier workers is justified, despite the close similarity of the two taxa (see p. 210). I would also agree with their suggestion that the resemblances are homoplastic ones, but not, as was also suggested, the results of convergent evolution.

What I would argue against is the reasoning used by those workers for separating the taxa at more than the species level, namely the level and nature of phyletic differences between the two cichlid faunas to which the taxa belong. There would seem to be no grounds for assuming that each lake flock is of monophyletic origin, or that each flock is, phylogenetically speaking, a natural group. On the contrary, there seem to be grounds for thinking that each flock is composed of several lineages, and that most of these lineages have a geographical distribution which cuts across the present day lake boundaries. This, of course is not to deny that some lineages may have evolved in, and are endemic to, a particular lake, or that some lineages may be common to only Lakes Malawi and Tanganyika (see p. 227).

Regan's (1922b:158) postulated half-a-dozen ancestors for the Malawi haplochromine flock could, in essence but perhaps not magnitude, be nearer the mark than his and other workers' ideas on the flock's monophyly (Regan, 1922a & b; Trewavas, 1935 & 1949; Greenwood, 1974), and may well represent the situation in other lakes as well (Greenwood, 1980). Only a great deal more, and critical, work on the cichlids of all three major lakes will serve to test those suggestions.

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